The oldest record of *Juniperoxylon*, a cupressaceous fossil wood from the Middle Triassic of Argentina

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Ruiz, D.P. and Bodnar, J. 2019. The oldest record of *Juniperoxylon*, a cupressaceous fossil wood from the Middle Triassic of Argentina. *Acta Palaeontologica Polonica* 64 (3): 481–488.

One of the oldest species of fossil woods with affinities to Cupressaceae is *Cupressinoxylon zamunerae* from the Ladinian, Middle Triassic of Argentina, but the generic assignment of this species was a subject of debate. The main character that is in conflict with *Cupressinoxylon* is the presence of ray tracheids in *C. zamunerae*, a character absent in the original diagnosis of the genus. In order to clarify this issue, original microscopic slides of the type materials were restudied herein, and also new sections and SEM samples were observed. The supposed ray tracheids turned out to be parenchyma cells. A new combination is established, relating *C. zamunerae* to *Juniperoxylon* due to the markedly pitted ray parenchyma cells walls. This fossil species is the first mention of *Juniperoxylon* from the Mesozoic of Gondwana and the oldest record worldwide until date.

Key words: Coniferales, Cupressaceae, *Juniperoxylon*, wood anatomy, Triassic, Cortaderita Formation, Argentina.

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Received 11 January 2019, accepted 18 March 2019, available online 23 July 2019.

Introduction

Triassic record of fossil woods with affinities to the family Cupressaceae is very scarce, with reports of *Cupressinoxylon zamunerae* Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015 and *Protojuniperoxylon ischigualastense* (Bonetti, 1966) Bodnar and Artabe, 2007, both from Argentina (Bonetti 1966; Bodnar and Artabe 2007; Bodnar et al. 2015), *Protochamaecyparixylon klitzschii* Giraud in Giraud and Hankel, 1985 from Chile (Lutz et al. 1999), and *Juniperoxylon* sp. and *Cupressinoxylon* sp. from France (Lemoigne 1967). From these, *Protochamaecyparixylon klitzschii* is of doubtful assignment and, both *Juniperoxylon* sp. and *Cupressinoxylon* sp. from France probably correspond to *Protocupressinoxylon* according to Barale (1987). In addition, the sediments in which the French specimens were found were assigned to the Lower Jurassic (Barale 1987).

Cupressinoxylon zamunerae is the oldest taxon related to the family, and constitutes the earliest record of the genus *Cupressinoxylon* Göppert, 1850 until today. However, the assignment of the species to this fossil-genus has been questioned by some authors (i.e., Brea et al. 2016; Ruiz et al. 2017) because the characters described in the specific diagnosis do not fit with those in the original generic diagnosis of Göppert (1850).

In order to clarify this controversy, the type material of *Cupressinoxylon zamunerae* is reanalyzed, the specific diagnosis is emended, and the generic assignment is changed and discussed. Furthermore, this revision provides more details about the systematic affiliation of this species.

Institutional abbreviations.—PBSJ, Palaeobotanical Collection of the Museo de Ciencias Naturales de San Juan, San Juan, Argentina.

Other abbreviations.—Cp, contiguity percentage index; RLS, radial longitudinal section; Si, seriation index; TLS, tangential longitudinal section; TS, transversal section.

Material and methods

The studied material corresponds to the type specimens of *Cupressinoxylon zamunerae* described by Bodnar et al. (2015). The samples are fossil trunks collected from the Cortaderita Formation (Middle Triassic, Sorocayense Group) at La Tinta creek, 8 km east of Barreal city, located in

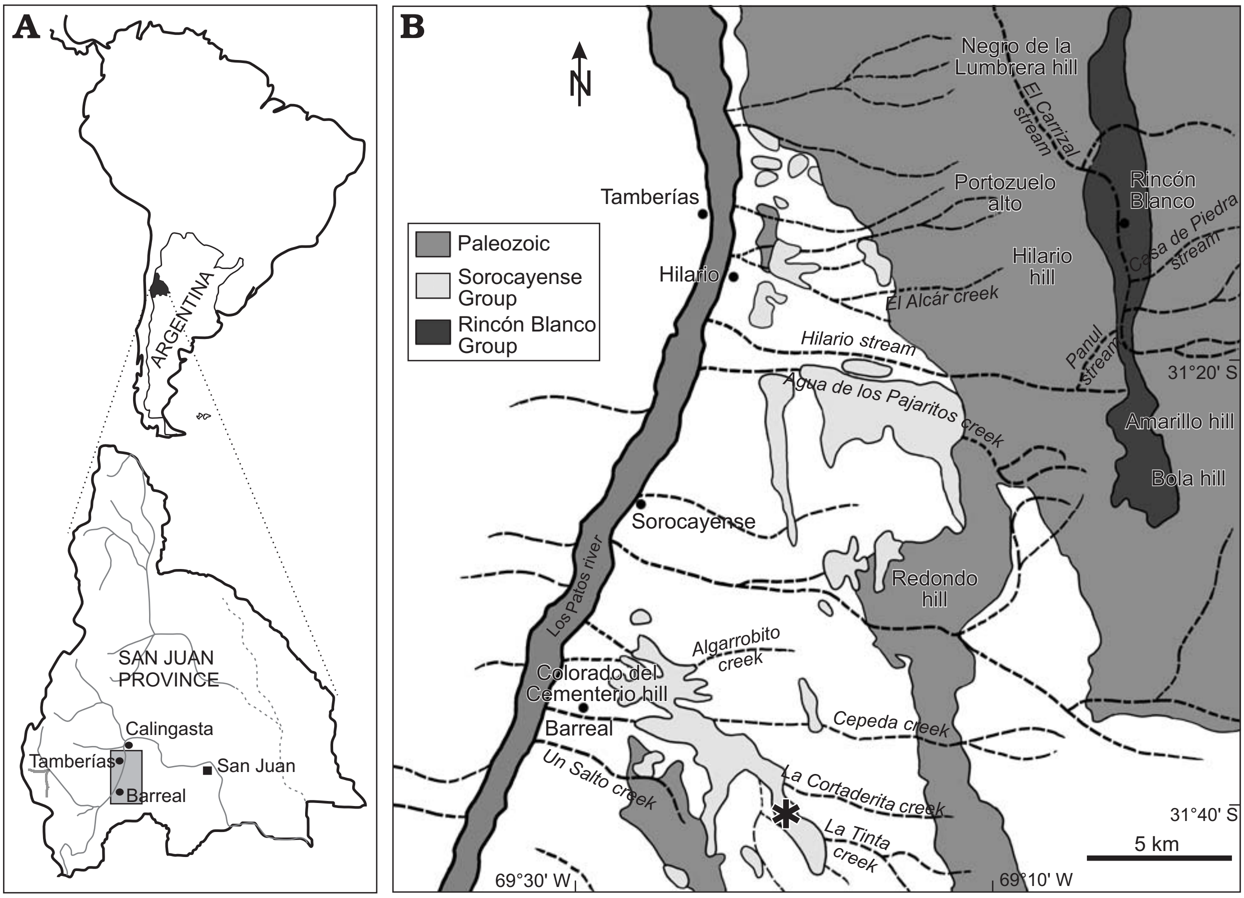

Fig. 1. **A**. Geographic location of study area at San Juan Province, Argentina. **C**. Geologic map showing the sampled locality (asterisk) at Cortaderita and La Tinta creeks, near Barreal town. Taken from Bodnar et al. (2018).

the western Precordillera, San Juan Province, central-western Argentina, between W 69°26′12.2′′ S 31°37′45.8′′ and W 69°23′52.1′′ S 31°39′00.1′′ (Fig. 1).

The samples are five permineralized woods housed at the Palaeobotanical Collection of the Museo de Ciencias Naturales de San Juan under the acronyms PBSJ 827 to PBSJ 831. Previous microscopic thin sections were revised and also new sections were made. Thin sections were studied using Leica DC 150 light microscopy. Small fragments of all of the woods were observed at SEM, mostly in longitudinal radial view.

A minimum of 30 measurements of each character were made. The measurements are expressed as the mean followed by the range between parentheses. The description was made following the terminology of Philippe (1995) and IAWA Committee (2004), and the Si and Cp indices of Pujana et al. (2016). For the suprageneric assignment the classification scheme of Anderson et al. (2007) was followed.

Systematic palaeontology

Order Pinales (= Coniferales) Gorozhankin, 1904

Family Cupressaceae Gray, 1822

Genus *Juniperoxylon* (Houlbert, 1910) Kräusel, 1949

Type species: Juniperoxylon turonense Houlbert, 1910; Miocene, Touraine, France.

Juniperoxylon zamunerae (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. emend.

Fig. 2.

2015 *Cupressinoxylon zamunerae*; Bodnar, Ruiz, Artabe, Morel, and Ganuza 2015: 149–150, fig. 5A–O.

Type material: Five pieces of different trunks and their thin sections. Holotype: PBSJ 828. Paratypes: PBSJ 827; PBSJ 829–831. There are three thin sections for each of the three sections (RLS, TLS, TS) used for anatomical studies.

Type locality: La Tinta creek, Barreal area, Barreal-Calingasta depocenter, Cuyo Basin, San Juan Province, Argentina.

Type horizon: EF6 and EF7, lower member of Cortaderita Formation, Ladinian (Middle Triassic) (Bodnar et al. 2019).

Emended diagnosis.—Abrupt transition from earlywood to latewood, narrow band of latewood. Abietinean radial pitting. Conspicuous torus. Axial parenchyma scarce, with smooth or irregularly thickened transverse end walls. Cross-fields with 1–2 oculipores of cupressoid type in one radial row. Homocelullar, mainly uniseriate rays of medium height.

Description.—Homoxylic and pycnoxylic seconday xylem. Transversal section: growth rings boundaries are distinct,

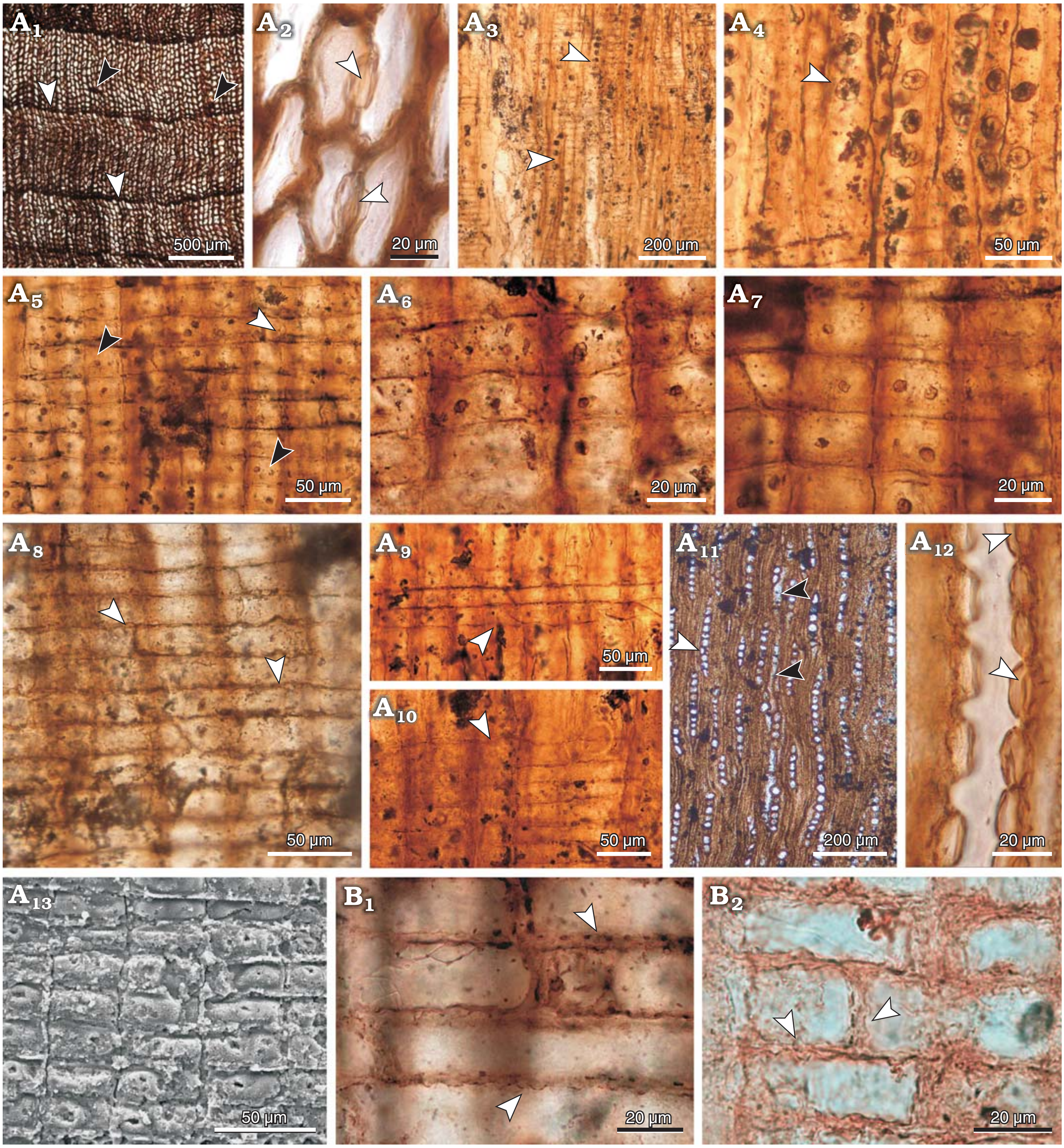

Fig. 2. Cupressaceous wood *Juniperoxylon zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. (holotype PBSJ 828, **A**; PBSJ 829, **B**), Cortaderita Formation, Middle Triassic of Argentina. A_1, growth rings (white arrowheads) and axial parenchyma (black arrowheads), TS; A_2, torus (arrowheads), TS; A_3, A_4, uniseriate or rarely biseriate radial pitting on tracheid walls (arrowheads), RLS; A_5, cupressoid cross-field pits (black arrowheads) and nodular end walls of ray parenchyma (white arrowheads), RLS; A_6, A_7, detail of cross-field pits, RLS; A_8, general view of ray parenchyma cells walls distinctly pitted (arrowheads), RLS; A_9, A_{10}, different ray parenchyma cells (arrowheads), RLS; A_{11}, occasional biseriation on part of a ray (white arrowhead) and axial parenchyma (black arrowhead), TLS; A_{12}, radial pits with torus (arrowheads), TLS; A_{13}, cross-field with cupressoid pits, RLS. B_1, B_2, ray parenchyma walls distinctly pitted (arrowheads), RLS.

with 1–3 cells of latewood (abrupt transition) (Fig. 2A_1). Tracheids are quadrangular in outline (Fig. 2A_1). Tangential diameter of tracheids is 26.5 µm (10.9–48.9 µm), and tracheid walls are 7.4 µm (4.2–10.9 µm) thick. Tracheid radial diameter is 34.5 μm (15.7–61 μm) in earlywood. Axial parenchyma is scarce (Fig. $2A_1$). Rays are separated from each other by 3 (1–6) rows of tracheids.

Radial longitudinal section: the wood has abietinean radial pitting, pits are circular, bordered, spaced (Cp = 21.4) and predominantly uniseriate (Si = 1), with occasional biseriation (Fig. $2A_3$, A_4). Only a few contiguous pits were observed. When biseriation occurs pits are opposite. Pits are 18.9 μm (13.1–25.5 μm) in radial diameter and 17.9 μm (14.9–22.6 μm) in vertical diameter, and pit apertures are 3.9 μm (3.2–4.6 μm) in vertical diameter. Torus is clearly seen (Fig. $2A_2$, A_{12}).

Rays are homocellular and parenchyma cells are rectangular (procumbent) with distinctly pitted horizontal and end walls (nodular) (Fig. $2A_8$, B). In some parts of the samples this character is hardly visible because of the poor preservation. End walls are straight (vertical or oblique) or occasionally concave or convex ("indented" in the original diagnosis). In some rays, marginal ray parenchyma cells have an irregular shape giving the appearance of ray tracheids (Fig. $2A_9$, A_{10}). These cells are higher, 24.3 μm (20.7–31.2 μm), than the other ray cells which are 14.9 μm (7.3–21.3 μm) high, but they are still of procumbent type. There are one or two (up to four) oculipores of the cupressoid type per cross-field (sensu IAWA 2004) (Fig. $2A_5$–A_7, A_{13}), with an oblique aperture of 5.8 μm (3.9–7.8 μm) in vertical diameter.

Tangential longitudinal section: rays are mostly uniseriate (93.3%) but some of them are partially biseriate (6.7%) (Fig. $2A_{11}$). Rays are 10 μm (1–34) cells and 210 μm (52–751) high. Ray cells are circular in tangential view and the lumen has a width of 11.1 μm (5.3–18.8 μm), with walls of 3.5 μm (2.3–4.8 μm) thick. Axial parenchyma is scarce and diffuse. The transverse end walls of the axial parenchyma are smooth or irregularly thickened (Fig. $2A_{11}$).

Stratigraphic and geographic range.—Ladinian, Middle Triassic, San Juan Province, Argentina.

Discussion

Generic assignment and comparisons.—According to Philippe and Bamford (2008), the fossil wood *Cupressinoxylon* is characterized by an usually narrow latewood with thick-walled flattened tracheids latewood and wide earlywood with thin-walled tracheids; pits round, uni- to quadriseriate and opposite, sometimes also on tangential walls; presence of axial parenchyma; low and uniseriate homocellular rays composed of pitted parenchyma cells; cupressoid cross-field with spaced oculipores in the earlywood usually ordered in rows and columns. However, several authors adopted a wider use of *Cupressinoxylon* (e.g., Müller-Stoll and Schultze-Motel 1990; Wang et al. 1996; Bamford et al. 2002) as a fossil-genus comprising those woods of Cupressaceae type which cannot be assigned to a more precise fossil-genus (sensu Vaudois and Privé 1971), considering it as a "wastebasket" taxon. The original diagnosis (Bodnar et al. 2015: 149) of *Cupressinoxylon zamunerae* characterized the species as it follows "Pycnoxylic homoxylic secondary wood with distinct growth rings of variable width [...] Tracheid pits in radial walls bordered, circular and spaced, predominantly uniseriate, with circular pore and conspicuous torus. Axial parenchyma scarce and diffuse. Cross-fields with 1–2 oculipores of cupressoid type, in one row. Heterocellular, mainly uniseriate, and 4–33 cells high rays. Ray cells with pitted horizontal walls, and thickened and indented end walls". This combination of characteristics led Bodnar et al. (2015) to assign the studied samples to *Cupressinoxylon* in the wider sense of Vaudois and Privé (1971).

Some authors have put in doubt the assignment of the studied species to *Cupressinoxylon* based on the presence of heterocellular rays (Brea et al. 2016; Ruiz et al. 2017). In the present revision of the type material of *Cupressinoxylon zamunerae*, the putative rays tracheids are considered as larger parenchyma cells with irregular shape but of the same type of the other ray cells (see description above), because they have identical walls and pits (Fig. $2A_9$, A_{10}). As a result, rays are herein reinterpreted as homocellular.

The character "indented" end walls on ray parenchyma cells, mentioned in the diagnosis of Bodnar et al. (2015), is not included in the present specific emendation in order to avoid confusion with the term "indentures" used in IAWA (2004).

Another trait that drew attention is the presence of ray parenchyma cells with terminal and horizontal walls distinctly pitted. This feature was included in the specific diagnosis of Bodnar et al. (2015), but only the horizontal walls of the ray cell were indicated as pitted. As seen in the Fig. $2B_2$, the end walls of ray parenchyma cells are also distinctly pitted (i.e., nodular). Two other fossil-genera of homoxylic wood with cupressoid cross-fields are characterized by the occurrence of nodular walls of ray parenchyma cells: i.e., *Protojuniperoxylon* and *Juniperoxylon* (Philippe and Bamford 2008). The abietinean pattern of radial tracheid pitting excludes the analyzed wood from *Protojuniperoxylon* which possesses mixed tracheid pitting (Table 1). As a consequence, we transferred *Cupressinoxylon zamunerae* to *Juniperoxylon* herein.

Houlbert (1910) erected the genus *Juniperoxylon* but he did not provide an appropriate diagnosis. Therefore, the protologue of Kräusel (1949) is in common use. It reads as follows: "Wood, similar to *Cupressinoxylon*. Ray cell walls, at least the terminal ones, more or less strongly pitted ("Juniperustüpfelung"), traumatic wood never with resin pockets" (Kräusel 1949: 177 [translated from the German]).

Approximately 19 species of *Juniperoxylon* have been described, mainly from Europe. From these, seven species were reassigned to another genera: *Juniperoxylon uralense* Jarmolenko, 1934b to *Cupressinoxylon* (Kräusel 1949), *Juniperoxylon turoviense* Kostyniuk, 1967, and *Juniperoxylon lusaticum* Kostyniuk, 1967 to *Taxodioxylon* (Süss and

Table 1. Comparison with the accepted species of *Juniperoxylon* and *Protojuniperoxylon*. References: Houlbert (1910), Stopes (1915), Eckhold (1923), Kräusel (1920, 1949), Stockmans and Wileière (1934), Grambast (1954), Bonetti (1966), Huard (1966), Van der Burgh (1973), Watari and Nishida (1973), Suess and Rathner (1998), Bodnar and Artabe (2007), Kłusek (2014), Dolezych (2016). Abbreviations: AP, axial parenchyma; C, crassulae; CFPT, cross field pit type; GR, distinct growth rings; RH, ray height (number of cells); RPEW, nodular ray parenchyma end walls; RPHW, ray parenchyma horizontal walls; RT, ray tracheids; RTP, radial tracheid pits; RW, ray width; +, present; –, absent; ± occasional; () characters which appear occasionally; ? unknown.

Species	Age and distribution	GR	Serration of RTP	Spacing of RTP	Arrangement of bi- or multi-seriate pits	AP	AP transverse end walls	RH	RW	RT	RPHW cells	RPEW cells	CFPT	C
Juniperoxylon breviparenchymatosum Watari and Nishida, 1973	Eocene; Japan	+	uniseriate. biseriate	spaced	opposite	abundant, diffuse and zonate	smooth or irregularly thickened	1–14	uniseriate, rarely partly biseriate	–	smooth or rarely pitted	+	2–6, taxodioid	–
Juniperoxylon juniperoides (Kownas, 1951) Huard, 1966	Miocene; Germany	+	uniseriate, biseriate	spaced	opposite	abundant, diffuse and zonate	nodular	1–12	uniseriate	–	distinctly pitted	+	1–4 (6), cupressoid	+
Juniperoxylon pachyderma (Göppert, 1850) Kräusel, 1949	Oligocene–Miocene; Germany, Belgium, Netherlands, Poland, Siberia	+	uniseriate, rarely biseriate triseriate	spaced	opposite	abundant, diffuse and zonate	smooth or nodular	1–15	uniseriate, rarely partly biseriate	–	smooth	+	1–6, cupressoid	+
Juniperoxylon pottoniense (Stopes, 1915) Kräusel, 1949	Early Cretaceous–Eocene; England, Denmark	+	uniseriate	spaced?	?	abundant, zonate	smooth?	1–12	uniseriate	–	distinctly pitted	+	cupressoid	–
Juniperoxylon rhenanurn Van der Burgh, 1973	Miocene; Germany	+	uniseriate, biseriate	spaced	opposite	present, diffuse and zonate	nodular	1–40	uniseriate, occasionally biseriate	±	distinctly pitted	+	1–3, cupressoid, taxodioid	+
Juniperoxylon schneiderianum Dolezych, 2016	Miocene; Germany	+	uniseriate, biseriate	spaced	opposite	abundant, diffuse	nodular	2–18	uniseriate, occasionally biseriate	–	sparsely pitted	+	2–4, taxodioid, cupressoid	+
Juniperoxylon turonense Houlbert, 1910	Eocene–Miocene; France	+	?	spaced?	?	present, diffuse	?	?	uniseriate	–?	distinctly pitted?	+?	cupressoid or taxodiod?	–?
Juniperoxylon wagneri Süss and Rather, 1998	Miocene; Germany	+	uniseriate, rarely biseriate	spaced	opposite	abundant, diffuse	nodular	1–5	uniseriate	–	smooth	+	2–8, cupressoid	–
Juniperoxylon zamunerae (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) Ruiz and Bodnar, 2019 (this paper)	Middle Triassic; Argentina	+	uniseriate, rarely biseriate	spaced	opposite	scarce, diffuse	smooth or irregularly thickened	2–34	uniseriate, rarely partly biseriate	–	distinctly pitted	+	1–2 (3–4), cupressoid	–
Protojuniperoxylon ischigualastense Bonetti, 1966 emend. Bodnar and Artabe, 2007	Late Triassic; Argentina	+	uniseriate, biseriate	spaced, contiguous	alternate, opposite	present, diffuse	smooth	1–45	uniseriate, less frequent partly bi- or triseriate	+	distinctly pitted	+	2–4, cupressoid	–
Protojuniperoxylon maidstonense (Stopes, 1915) Eckhold, 1923	Lower Cretaceous; England	+	uniseriate	spaced, contiguous	?	absent or scarce, diffuse	?	1–20	uniseriate, rarely partly biseriate	–	smooth?	+	4–6, cupressoid	+

Table 2. Comparison of *Juniperoxylon zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. with selected extant genera of Cupressaceae sensu lato. Abbreviations: GR, growth rings; AT, axial tracheid; ATTP, axial tracheid tangential pitting; AP, axial parenchyma; RW, ray width; RH, ray height; RPEW, ray parenchyma cells end walls; RPHW, ray parenchyma horizontal walls; IN, indentures; CFPT, cross field pit type, CFPN, cross field pit number; RT, ray tracheids; + present; – absent; () characters which appear occasionally. From Román-Jordán et al. (2017) and Nunes et al. (2019).

Taxa	Distribution	GR	AT cross sections	AT radial pitting	ATTP	AP	AP walls	AP arrangement	RW	RH	RPEW	RPHW	IN	CFPT	CFPN	RT
Calocedrus	USA, China, Thailand, Birmania, Laos, Vietnam	well or slightly defined	polygonal	uniseriate, (biseriate)	+	+	irregularly thickened, nodular	diffuse, tangentially zonate or marginal	uniseriate and partially biseriate	1–15	smooth or nodular	pitted or unpitted	+	cupressoid	1–4 (7)	–
Chamaecyparis	USA, Japan, Taiwan	well defined	circular or polygonal	uniseriate	– or +	– or +	smooth or nodular	diffuse or tangentially zonate	uniseriate and partially biseriate	1–15 (25)	smooth or nodular	pitted or unpitted	– or +	cupressoid or taxodioid	1– 4 (7)	– or +
Cupressus	temperate regions of Northern Hemisphere	well or slightly defined	circular or polygonal	uniseriate	+	scarce or +	smooth or irregularly thickened, nodular	diffuse, tangentially zonate or marginal	uniseriate and partially biseriate	1–15 (45)	smooth or nodular	pitted or unpitted	+	cupressoid	1–4 (6)	– or +
Fitzroya	Argentina, Chile	well defined	polygonal	uniseriate	+	+	(smooth), irregularly thickened, nodular	diffuse or tangentially zonate	uniseriate	1–15 (19)	smooth or nodular	pitted or unpitted	+	cupressoid	1–4 (8)	– or (+)
Juniperus	Northern Hemisphere	well defined	circular or polygonal	uniseriate, (biseriate)	+	scarce or +	smooth or irregularly thickened, nodular	diffuse, tangentially zonate or marginal	uniseriate and partially biseriate	1–14 (24)	smooth or nodular	pitted or unpitted	+	cupressoid	1–4 (8)	–
Sequoiadendron	USA	well defined	polygonal	uniseriate (biseriate)	+	+	smooth or irregularly thickened, nodular	diffuse or marginal	uniseriate and partially biseriate	130	smooth	pitted or unpitted	–	cupressoid and (taxodioid)	1–2	–
Taxodium	USA, Mexico	well defined	polygonal	uniseriate, biseriate	+	+	(smooth) nodular	diffuse or tangentially zonate	uniseriate and partially biseriate	1– 30	smooth	(pitted) or unpitted	–	cupressoid and taxodioid	1–4 (8)	–
Juniperoxylon zamunerae	Argentina	well defined	polygonal (quadrangular)	uniseriate, (biseriate)	–	scarce	smooth or irregularly thickened	diffuse	uniseriate (partially biseriate)	1–34	nodular	pitted	–	cupressoid	1–2 (4)	–

Rathner 1998; Kłusek 2014); *Juniperoxylon glyptostroboides* Kostyniuk, 1967 to *Glyptostroboxylon* (Dolezych and Van der Burgh 2004), *Juniperoxylon sibiricum* Nastschokin, 1962 to *Cedroxylon* (Süss and Rathner 1998); *Juniperoxylon lignieri* Grambast, 1954 to *Prototaxodioxylon* (Süss and Rathner 1998); and *Juniperoxylon barbaricinum* Charrier, 1961 to *Brachyoxylon* (Philippe et al. 2004). On the other hand, *Juniperoxylon silesiacum* (Prill, 1913) Kräusel, 1920, *Juniperoxylon pauciporosum* (Prill, 1913) Kräusel, 1920, *Juniperoxylon kalickiji* Jarmolenko, 1934a, and *Juniperoxylon neosibiricum* (Schmalhausen, 1890) Selling, 1944 were synonimized with *Juniperoxylon pachyderma* (Göppert, 1850) Kräusel, 1949 (Kräusel 1949; Kłusek 2014). In this manner, only eight species are currently accepted within *Juniperoxylon*. In comparison with these taxa, *Juniperoxylon zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb nov. is distinguishable due to the ray height (up to 34 cells) and the scarce axial parenchyma. The only species with similar ray height (up to 40 cells) is *J. rhenanurn* Van der Burgh, 1973 from the Miocene of Germany, but it differs from the Argentinean wood because of the presence of crassulae and occasional ray tracheids (Table 1).

The record of *Juniperoxylon* is mainly restricted to Cenozoic, with only two reports from the Mesozoic: *Juniperoxylon* sp. from the Early Jurassic of France (Lemoigne 1967; Barale 1987) (of doubtful assignment), and *Juniperoxylon pottoniense* (Stopes, 1915) Kräusel, 1949 from the Lower Cretaceous of England (Stopes 1915; Kräusel 1949). The only species described as a *Juniperoxylon* from Gondwanan is *Juniperoxylon barbaricinum* Charrier, 1961, from Sardinia, Italy, but the determination was rejected by Bamford and Philippe (2001) and Philippe et al. (2004), because it presents mixed tracheid pitting and lacks of pits or thickenings on the end walls of ray cells. Thus, *J. zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. would be the first record of *Juniperoxylon* for the Mesozoic of Gondwana, and the earliest record of the genus worldwide until date.

Systematic affiliation.—*Juniperoxylon* has been related to the Cupressaceae (Vaudois and Privé 1971; Bodnar and Artabe 2007; Kłusek 2014; Dolezych 2016) due to the presence of abietinean tracheid pitting, distinctly pitted ray cell walls, axial parenchyma and cupressoid cross-fields, and the absence of normal resin canals and helical thickenings.

In particular, *Juniperoxylon zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. shows characters which relate it to different genera of living Cupressaceae (Table 2). The distinctly pitted end and horizontal walls of ray parenchyma cells relate this fossil wood to genera of Cupressaceae sensu stricto (i.e., *Calocedrus*, *Chamaeocyparis*, *Cupressus*, *Fitzroya*, and *Juniperus*), while the ray height (1–34 cells high) link it to genera belonging to the basal Cupressaceae (formerly Taxodiaceae) (i.e., *Sequoiadendron* and *Taxodium*) (Table 2). If *J. zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. corresponds to one of the oldest fossil related to the Cupressaceae, its characteristics could indicate that the earliest representatives of the family would have shared wood traits with both basal and derived Cupressaceae.

Conclusions

The systematic revision of the type specimens of *Cupressinoxylon zamunerae* revealed that: (i) the ray cells previously interpreted as tracheids are actually parenchyma cells with a different morphology than the others; and (ii) distinctly pitted walls of ray parenchyma cells indicate that the fossil wood is accurately assigned to *Juniperoxylon*. With the new combination, this species constitutes the first record of *Juniperoxylon* from the Mesozoic of Gondwana and the oldest record worldwide until today. *Juniperoxylon zamunerae* (Bodnar, Ruiz, Artabe, Morel, and Ganuza, 2015) comb. nov. has a combination of anatomical characters that allow us to assign it to the Cupressaceae, and probably represents one of the earliest record of the family.

Acknowledgments

We thank to Roberto R. Pujana (Museo Argentino de Ciencias Naturales-CONICET, Buenos Aires, Argentina) for the help in the preparation of the new microscopic thin sections and the comments on the manuscript, and to the electronic microscopy service of the Museo Argentino de Ciencias Naturales-CONICET. The editor and two anonymous reviewers are specially thanked for their helpful comments and suggestions. This study was supported by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2014-2751) and Universidad Nacional de La Plata (Project N807).

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